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A new large-sized lepetid limpet from the abyssal northwestern Pacific is the deepest known patellogastropod

Chong Chen[1], Miwako Tsuda[2], Yoshiyuki Ishitani[1]

1 *X-STAR, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan*

2 *Project Team for Development of New-Generation Research Protocol for Submarine Resources, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, 237-0061, Yokosuka, Kanagawa, Japan*

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Corresponding author: Chong Chen (cchen@jamstec.go.jp)

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Abstract

True limpets in the gastropod subclass Patellogastropoda are familiar members of shallow-water rocky environments but are much rarer in the deep, with just three families adapted to bathyal depths or more. Of these, Lepetidae is the only one found on ambient seafloor habitats, and *Bathylepeta* is a very deep genus known from two species off Chile and Antarctica. Here, we report a giant *Bathylepeta* up to a shell length of 40.5 mm from 5922 m deep in the northwestern Pacific and name it *Bathylepeta wadatsumi* **sp. nov.** Phylogenetic reconstruction using the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene supports the placement of this new species in *Bathylepeta*. Our new species is most similar to *B. linseae* from the Weddell Sea but can be distinguished by its much more developed second lateral and marginal teeth, as well as a larger size. *Bathylepeta wadatsumi* **sp. nov.** also has slightly imbricating radular basal plates, a feature previously unknown from this genus; we therefore emend the genus diagnosis. Our finding not only extends the distribution of this enigmatic limpet genus to Japan but also marks the deepest bathymetric record for the entire Patellogastropoda.

Key Words

COI mtDNA, Gastropoda, Lepetidae, Mollusca, morphology, new species, Patellogastropoda, phylogeny, taxonomy

Introduction

The subclass Patellogastropoda, commonly known as true limpets, is a major group of marine gastropods characterised by their cap-like shells and typically inhabit hard substrates (Ponder et al. 2020). While most patellogastropods are familiar inhabitants of intertidal zones and other shallow-water systems, three families – Lepetidae, Neolepetopsidae, and Pectinodontidae – have successfully colonised deep-sea environments (Nakano and Ozawa 2007). Recent phylogenomic analyses have revealed these three families to represent a monophyletic clade and thus a single deep-water colonisation event (Qi et al. 2024). Two of these families specialise in chemosynthetic biological hotspots, with Neolepetopsidae found in inactive and active hydrothermal vent chimneys as well as hydrocarbon seeps, and Pectinodontidae inhabiting sunken wood, hydrothermal vents, and hydrocarbon seeps (Chen et al. 2019; Chen et al. 2021). As such, Lepetidae is the only family of true limpets that occurs on the vast 'normal' deep seafloor, where it extends into the abyssal plains beyond a depth of 5000 m (Moskalev 1977).

The lepetid genus *Bathylepeta* was established for the deepest known true limpet species, *Bathylepeta laevis* Moskalev, 1977, from off Chile in the southeastern Pacific Ocean at 5300–5320 m deep (Moskalev 1977). A second species, *Bathylepeta linseae* Schwabe, 2006, was later described from the Weddell Sea in Antarctica, where it has been collected between 2084 m and 4805 m, extending the known distribution of the genus (Schwabe 2006; Warén et al. 2011). Morphologically, this genus is currently diagnosed by an oval aperture outline, a postcentral apex, and non-imbricating basal plates on the radula. Members of this genus are notable not only for their

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very deep habitats but also for their large size considering the depth, with *B. laevis* reaching 30 mm in shell length. Both species were collected by towed sampling gears and supposedly on sediments; little is known about their habitat and ecology.

Here, we report the discovery of a third *Bathylepeta* species, from the northwestern Pacific at a depth of 5922 m, greatly extending the range of this mythical genus. This species was collected by a manned submersible, providing valuable information on the ecology of *Bathylepeta*.

Materials and methods

Specimen collection and seafloor imagery

A patellogastropod limpet was obtained from a rocky substrate on a graben escarpment in the abyssal northwestern Pacific (Figs 1, 2), approximately 500 kilometres southeast of Tokyo, Japan. A suction sampler attached to the human-occupied vehicle (HOV) *Shinkai 6500*, deployed from the research vessel R/V *Yokosuka*, was used to collect the specimen. A digital single-lens reflex camera (Canon EOS 5D Mark II with EF 16–35 mm 1:2.8 L II USM lens) was used to photograph the seafloor through the porthole of *Shinkai 6500*. A digital still camera (Olympus E-PL6, 16 megapixels) mounted outside the submersible was also used.

Morphological examination

Upon retrieval of the submersible, the limpet was cleaned using nylon brushes and then photographed using a Canon EOS 5Ds R digital single-lens reflex camera equipped with an EF 100 mm F2.8L Macro IS USM lens. Multiple focal planes were photographed and combined using Adobe Photoshop CC for focus-stacked images. Subsequently, the limpet was preserved in 70% ethanol for further analysis in shore-based laboratories. The limpet's external features were studied under a stereo microscope (Olympus SZX9), with soft parts removed from the shell using fine tweezers and spring scissors. Shell length (SL), shell width (SW), and shell height (SH) were measured with digital vernier callipers, rounded to the nearest 0.1 mm. Close-up photographs were taken using a Keyence VHX-S770E digital microscope with a VHX-E100 lens, with automatic image stacking by the built-in stacking function. Anatomical terminology follows Schwabe (2006) and Warén et al. (2011).

Scanning electron microscopy (SEM)

For SEM observation, the radula was extracted by dissecting the radula sac and dissolving surrounding tissues in a 10% commercial bleach solution. After sufficient dissolution, the radula ribbon was rinsed twice with MilliQ water and then twice with 99% ethanol. Mounting on aluminium stubs was done using conductive carbon tape, and the radula was air-dried before SEM observation. Observations were made using a Hitachi TM-3000 tabletop SEM at an acceleration voltage of 15 kV, without coating.

DNA barcoding

Genomic DNA was extracted from a piece of mantle tissue using the Takara Bio NucleoSpin Tissue kit, following the manufacturer's instructions. The mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene was amplified using the primer pair LCO1490 (5′–GGTCAACAAATCATAAAGATATTGG–3′) and HCO2198 (5′–TAAACTTCAGGGTGACCAAAAAATCA–3′) from Folmer et al. (1994). Standard methods for DNA amplification by polymerase chain reactions were carried out following Chen et al. (2015), and successful products were sent to FASMAC Corporation (Kanagawa, Japan) for bidirectional Sanger sequencing using the same primers. The resulting *COI* sequence was submitted to NCBI GenBank under the accession number PV528950.

Phylogenetic analysis

The *COI* sequence obtained from the limpet was analysed alongside other Lepetidae sequences available on GenBank. Two limpets from the closely related family Pectinodontidae were used as the outgroup (Qi et al. 2024; Warén et al. 2011). Sequence alignment was performed using the MUSCLE algorithm (Edgar 2004) within Geneious Prime 2025.0 (https://www.geneious.com/), resulting in a 584 bp alignment for further analysis.

Phylogenetic relationships were inferred using Bayesian methods implemented in MrBayes v3.2.6 (Ronquist et al. 2012). PartitionFinder v2.1.1 (Lanfear et al. 2017) determined the best-fit model under the Bayesian Information Criterion: GTR+I+G for the first and second codon positions and HKY+I+G for the third codon position. As the fast-evolving third codon position of the *COI* gene is known to be problematic in phylogenetic analysis of Patellogastropoda (Chen et al. 2021; Nakano and Ozawa 2007), this codon was removed from the analysis. Metropolis-coupled Markov Chain Monte Carlo simulations were run for one million generations, sampling every 1,000 generations. Tracer v1.7 (Rambaut et al. 2018) was used to assess convergence and determine an appropriate burn-in of 3,000. The consensus tree obtained was visualised using FigTree v1.4.4 and then finalised in Adobe Illustrator CC. Pairwise genetic distances among the two *Bathylepeta* species, including *B. linseae* (GenBank accession AB543973) and our new species (GenBank accession PV528950), were calculated using a 658 bp alignment in MEGA7 (Kumar et al. 2016) with the Kimura two-parameter model (Kimura 1980).

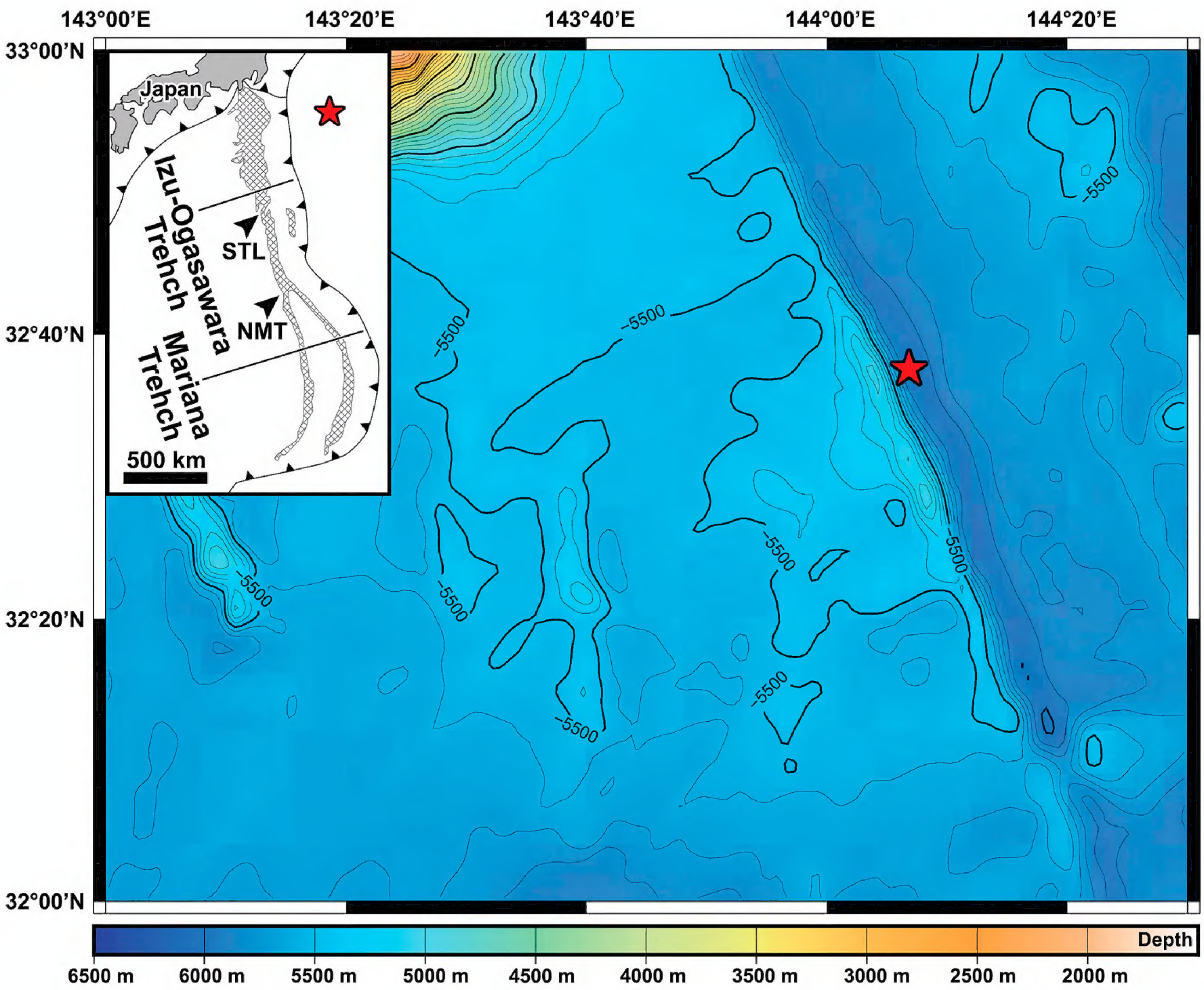

Figure 1. Map of the sampling locality (red star). On the western escarpment of a graben structure in the northwestern Pacific (32°37.0617'N, 144°6.5835'E, 5922 m deep), 500 km southeast of Tokyo, Japan. The inset shows the general location with Japan as a reference. Abbreviations: STL, Sofugan Tectonic Line; NMT, northern limit of Mariana Trough. Bathymetric data were retrieved from GEBCO 2023 (https://www.gebco.net/).

Results

Systematics

Subclass Patellogastropoda Lindberg, 1986
Superfamily Lottioidea Gray, 1840
Family Lepetidae Gray, 1850

***Bathylepeta* Moskalev, 1977**

Type species. *Bathylepeta laevis* Moskalev, 1977, by original designation.

Diagnosis. Emended based on results of this study after Moskalev (1977) and Schwabe (2006): Lepetid limpet with oval aperture outline, apex at postcentral position directed posteriorly, radula basal plates slightly overlapping to non-overlapping, marginal teeth with serrated or smooth edges.

Included species. *Bathylepeta laevis* Moskalev, 1977; *Bathylepeta linseae* Schwabe, 2006; *Bathylepeta wadatsumi* sp. nov.

***Bathylepeta wadatsumi* sp. nov.**

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Figs 2–4

Type locality. On shelf-like volcanic rock, on the western escarpment of a graben structure in the northwestern Pacific (32°37.0617'N, 144°6.5835'E, 5922 m deep), 500 km southeast of Tokyo, Japan (Figs 1, 2).

Type material. ***Holotype.*** (NSMT-Mo 79627), female; SL 40.5 mm, SW 33.4 mm, SH 18.8 mm, preserved in 70% ethanol. Taken by a suction sampler mounted onboard HOV *Shinkai 6500* from the type locality.

Diagnosis. A very large (at least up to 40.5 mm SL) *Bathylepeta* with about 80 clearly defined white radial streaks on the shell. When alive, ventral tissue generally pigmented reddish brown, oral shield greyish, oral lappets also reddish brown. Second lateral teeth very well-developed, each as large as the fused pair of first laterals. Basal plate rectangular, slightly overlapping. Marginal teeth also very well-developed, forming overhanging, spoon-like cusps larger in size than the laterals, edges smooth.

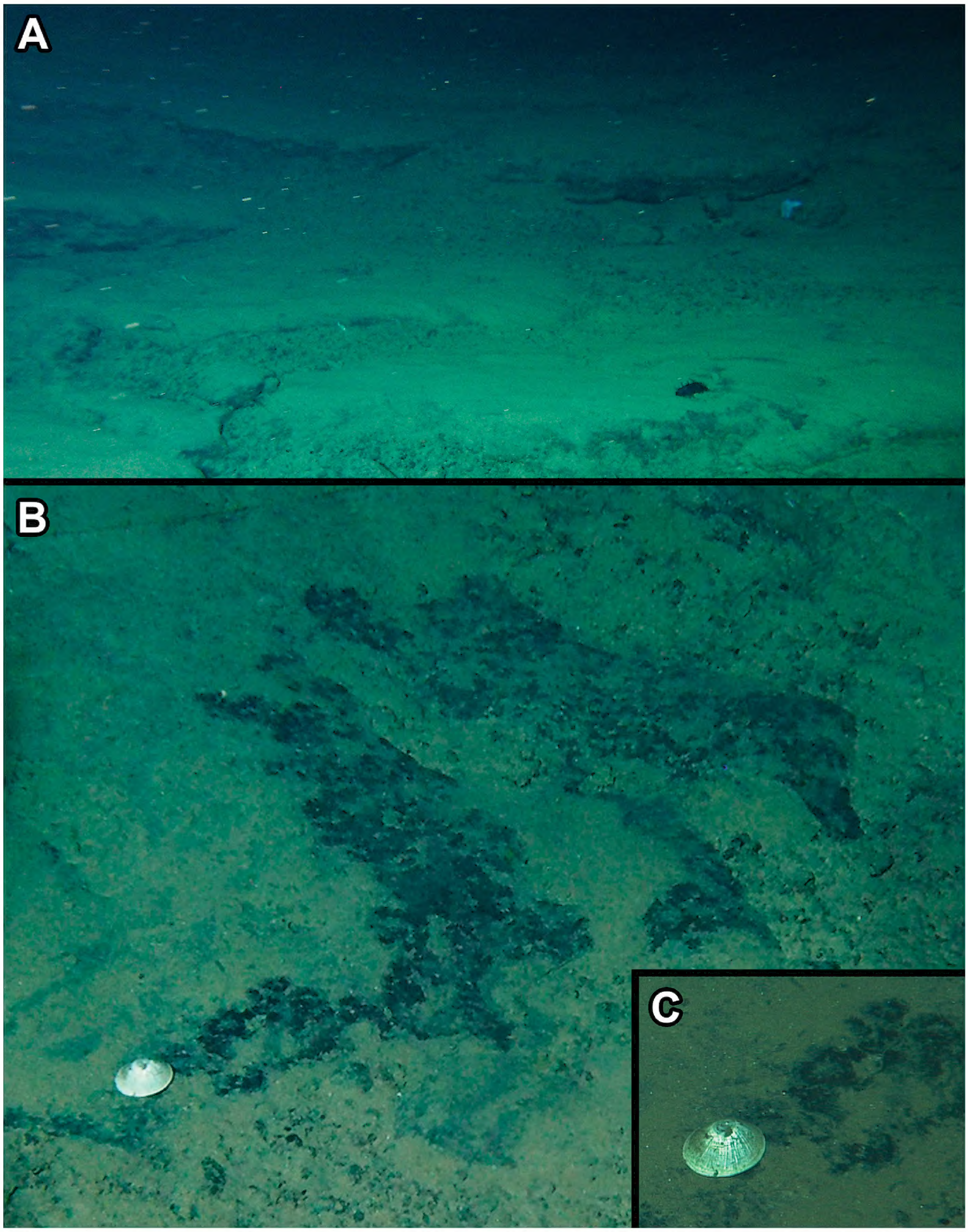

Figure 2. *In situ* imagery at the type locality of *Bathylepeta wadatsumi* sp. nov. **A.** General overview of the area with shelf-like volcanic rocks covered by a thin layer of sediment; **B.** Habitus of the holotype specimen with a clear feeding trail behind; **C.** is a close-up showing better details of the shell morphology. The shell length of the holotype is 40.5 mm.

Jaw strongly mineralised and reinforced. Genital papillae small, about 0.7 mm long when alive and contracted.

Description. Shell (Fig. 3) large (holotype 40.5 mm SL), limpet-formed, thin, translucent, bluish-grey, slightly elastic, possibly reflecting high organic content. Shell height nearly half of shell length. Apex postcentral at just behind centre of shell, strongly corroded, likely due to abyssal habitat below calcium compensation depth. Entire shell with fine concentric growth lines, crossed by about 80 clearly defined white radial streaks that decrease in strength outwards (Fig. 3C). Aperture broad oval, rate of widening increases from the final one-fourth of shell

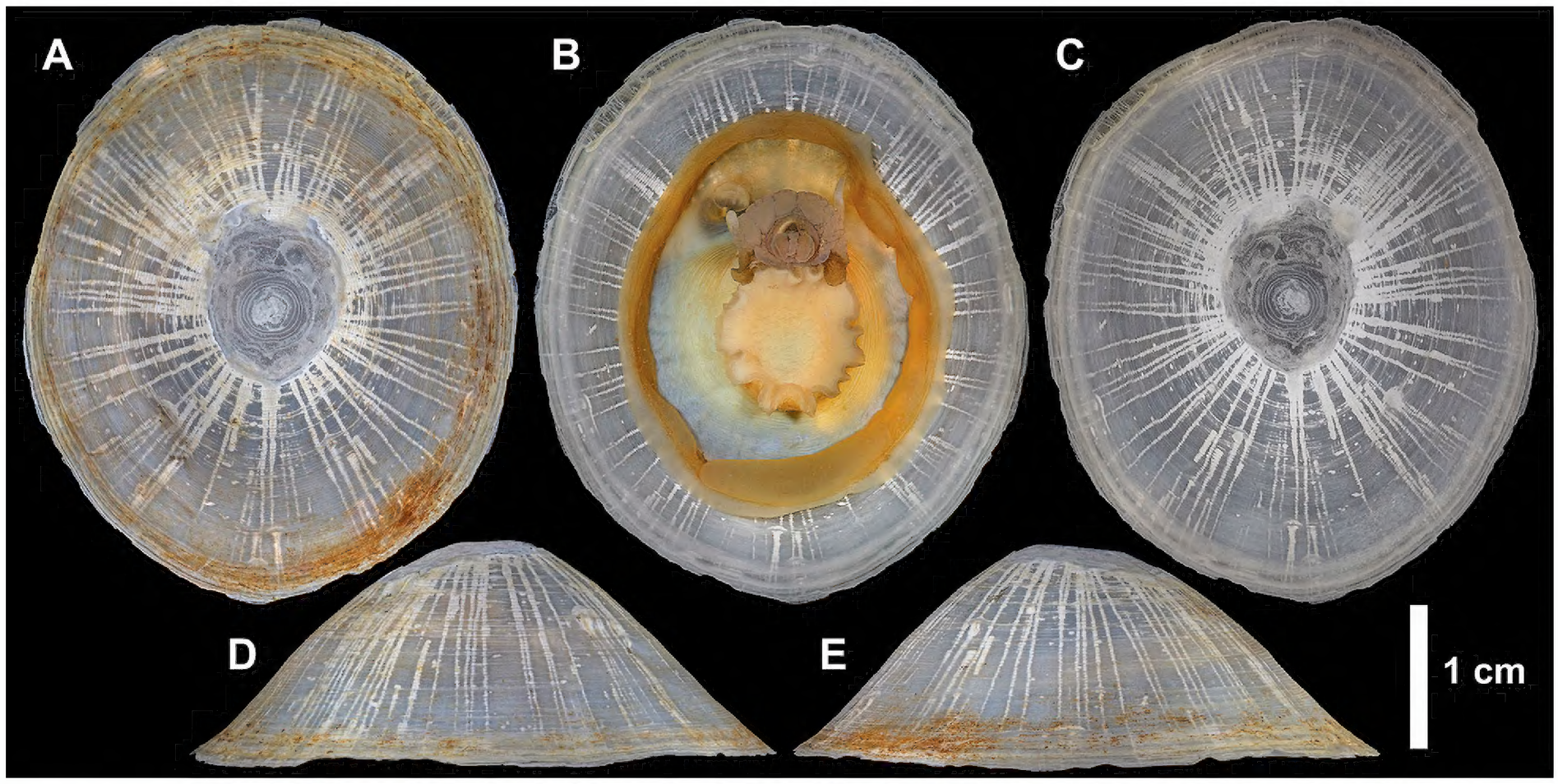

Figure 3. *Bathylepeta wadatsumi* sp. nov., holotype (NSMT-Mo 79627). **A**. Dorsal view; **B.** Ventral view; **C.** Ventral view with the soft parts removed; **D.** Lateral view from the left; **E.** Lateral view from the right.

growth (Fig. 3D–E). Shell margin not thickened, with sharp edge, margin smooth, uninterrupted. Protoconch corroded away in holotype.

Jaw plate (Fig. 4A) very sturdy, off-white, heavily mineralised, about 4 mm wide (mineralised part 2 mm wide). Cutting-edge U-shaped central part further reinforced with chitinous plates on inner side.

Radula (Fig. 4B–H) docoglossate, formula 2-2-0-2-2. Rachidian tooth lacking. Central element comprising two pairs of lateral teeth. First pair of lateral teeth fused together to form sharply pointed cusp with faint line at centre where fusion occur; bluntly pointed with overhanging, smooth cutting edges. Second laterals well-developed, each as large as fused pair of first laterals, with triangular, sharply pointed cusps with smooth cutting edge, pointed upwards at much higher angle compared to first laterals. Cusps of all laterals dark in colour, indicative of reinforcement by iron oxide (goethite), as for most other patellogastropod limpets. Basal plates underneath laterals whitish in colour (likely indicative of calcification), rectangular in outline, slightly imbricating with adjacent plates. Marginal teeth chitinous, translucent, strongly curved distally. Cusps of marginals well-developed, with broad, spoon-like overhanging morphology carrying rounded, smooth cutting edges. Marginal cusps much larger than those of laterals. Inner marginal (Fig. 4H) slightly wider than outer marginal (Fig. 4G), with broader shaft.

External anatomy (Fig. 5) when alive shows strong reddish-brown pigmentation when viewed ventrally, especially on inner fold of mantle edge; oral shield greyish in colour. Foot cream, lacking colouration. Mouth large, rounded with well-sized oral shield, containing heavily mineralised jaw. Oral lappets present on both sides of oral shield, large, reddish brown when alive. Pigmented eyes lacking. Cephalic tentacles simple, conical, elongate, tapering to a fine tip distally. Mantle edge thick, undulating, smooth, tentacles lacking. Mantle cavity shallow around foot, depressed in cephalic region. Genital papillae (Fig. 5E) present on right side, posterodorsal to right cephalic tentacle, located just right of anus, rather short at about 0.7 mm long when retracted and alive. Foot oval, fleshy, with undulating edge when contracted. Shell muscle horseshoe-shaped, occupying posterior two-thirds of body, split into numerous distinct muscular bundles.

Dorsal aspect of soft parts seen through mantle roof (Fig. 5D) largely occupied by very voluminous, dark-brown digestive gland. Intestine forms three loops, last two loops embedded in digestive gland. Final loop exits digestive gland from left side of mantle roof as rectum. Gonad (Fig. 5A) voluminous, positioned anteroventral of digestive gland and final loop of intestine. Gonad of holotype slightly damaged during collection, with some oocysts emerging; thus, holotype is female, assuming gonochorism like most other patellogastropod limpets. Ctenidium absent.

Etymology. From '*Wadatsumi*', god of the sea in Japanese mythology, alluding to its very deep habitat. It is also a reference to the fish-man character "*Large Monk*" *Wadatsumi* from Eiichiro Oda's manga series "ONE PIECE" (Oda 2011), whose enormous body size is reminiscent of the large size that *B. wadatsumi* sp. nov. reaches for a deep-water patellogastropod. Used as a noun in apposition.

Distribution. Only known from the type locality at 5922 m deep, living on hard volcanic rock covered by a thin layer of sediment (Fig. 1B). A winding feeding trail is clearly visible posterior to the limpet, indicating it feeds on this sediment layer. Several individuals were sighted from the viewport of the submersible, but only one individual (the holotype) was successfully collected.

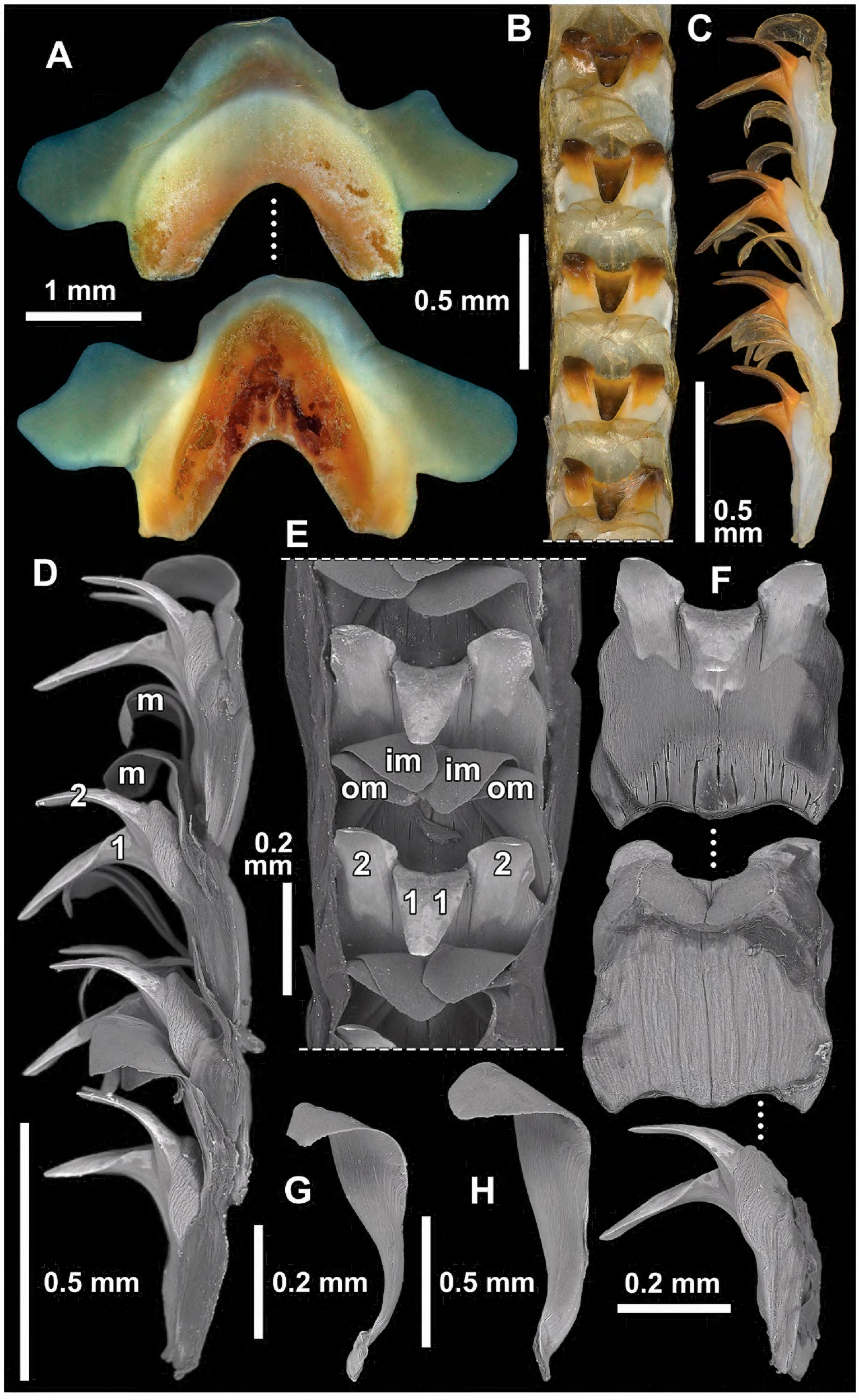

Figure 4. *Bathylepeta wadatsumi* sp. nov., jaw and radula of the holotype (NSMT-Mo 79627). **A.** Jaw viewed from the outside (above) and inside (below), the chitinous membrane is slightly damaged on the right side of the outside view; **B.** A section of the radula ribbon under a light microscope, showing dark tips of the lateral teeth indicative of iron oxide (goethite) mineralisation, with **C.** being a view from the side. **D.** The same radula section as **C.** but viewed under SEM. **E.** The same radula section as **B.** viewed under SEM. **F.** An isolated basal plate with the two lateral pairs attached, viewed from the front (top), back (middle), and side (bottom). **G**. An isolated feather-like outer marginal tooth. **H.** An isolated feather-like inner marginal tooth. Abbreviations: 1, first lateral tooth; 2, second lateral tooth; im, inner marginal; om, outer marginal; m, marginal teeth.

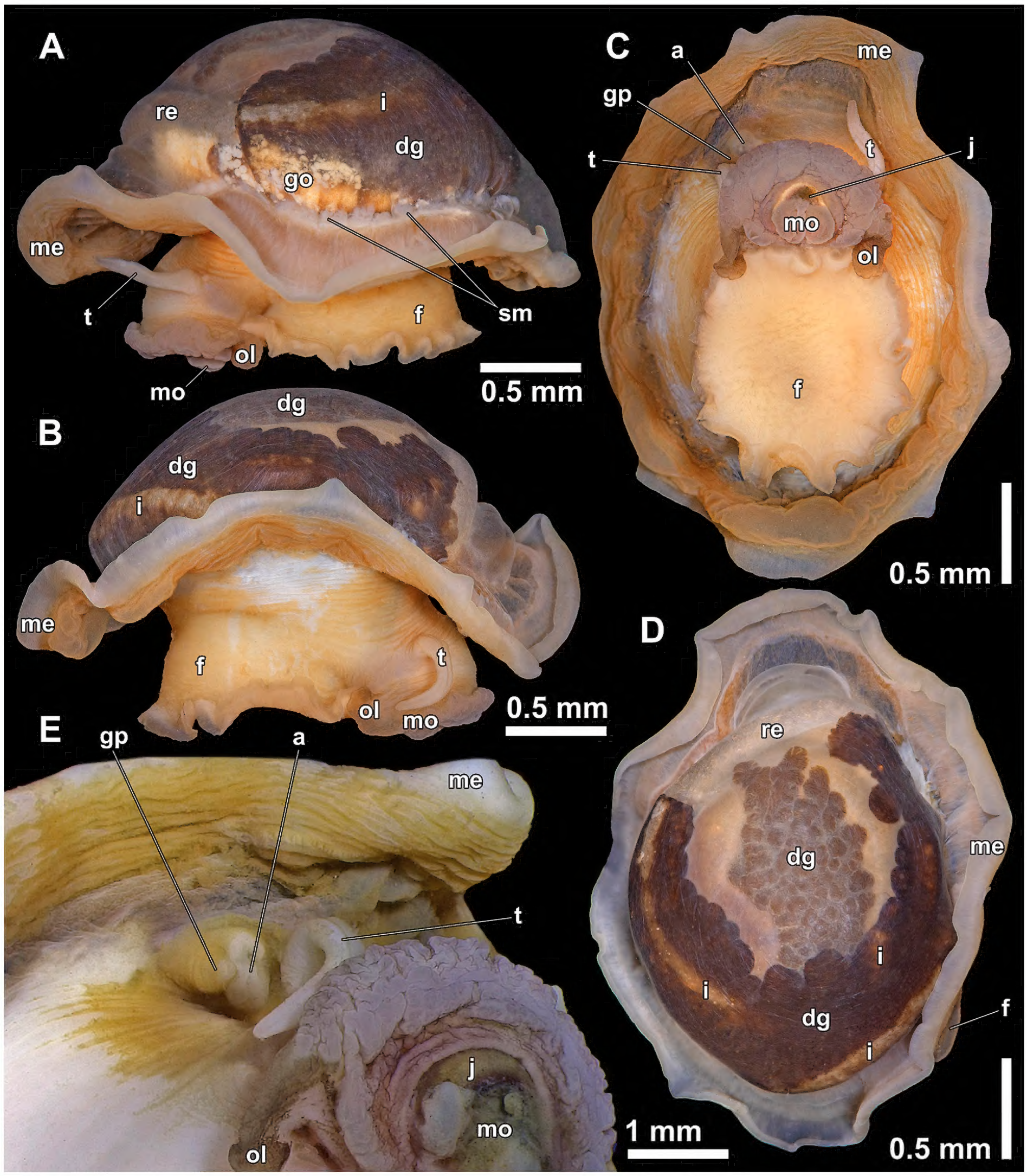

Figure 5. *Bathylepeta wadatsumi* sp. nov., external anatomy of the holotype (NSMT-Mo 79627). **A.** Soft parts viewed laterally from the left (note the gonad was slightly damaged during collection and some oocytes are emerging from the left side); **B.** the same viewed laterally from the right; **C.** ventral view; **D.** dorsal view. **E.** Close-up of the genital papillae. Abbreviations: a, anus; dg, digestive gland; f, foot; go, gonad; gp, genital papilla; i, intestine; j, jaw; me, mantle edge; mo, mouth; ol, oral lappet; re, rectum; sm, shell muscle; t, cephalic tentacle.

Remarks. *Bathylepeta wadatsumi* sp. nov. is unique among the genus in having the radular basal plates slightly imbricating and overlapping with adjacent ones (Fig. 5C), but all other aspects of shell and radular morphology agree with the other two described *Bathylepeta* species; its placement in this genus is also supported by molecular data (Fig. 6, see below). As such, we here emend the diagnosis for *Bathylepeta* to include slightly overlapping to non-overlapping basal plates. This feature thus separates *B. wadatsumi* sp. nov. easily from the other two described congeners.

Bathylepeta wadatsumi sp. nov. is most similar to *B. linseae* from the Weddell Sea in Antarctica in shell morphology, with both species carrying whitish radial rays on the shell surface that are missing in *B. laevis* (Moskalev 1977; Schwabe 2006). However, the radial rays are more clearly defined and numerous in *B. wadatsumi* sp. nov. compared

to *B. linseae* (about 80 vs 50). Due to the small number of specimens available, it is currently unclear how much intraspecific variation there is in these radial rays or if their formation is determined environmentally. These two species are also very different in other radular characters, where the second lateral and marginals are both strongly reduced in *B. linseae* but very well-developed in *B. wadatsumi* sp. nov. The marginals of *B. linseae* are hook-like and interpreted as function uncini (Lindberg 1998; Schwabe 2006), whereas in *B. wadatsumi* sp. nov. they are broad and spoon-like. Radular features other than the imbricating basal plates can also easily differentiate *B. wadatsumi* sp. nov. from *B. laevis*, in that *B. laevis* has much smaller second laterals, its marginal teeth carry denticulate and serrated cusps, and its basal plate is widened posteriorly rather than rectangular (Moskalev 1977). Furthermore, the shells of both *B. wadatsumi* sp. nov. and *B. linseae* are bluish-grey, whereas *B. laevis* is whitish-grey.

Genetic support

Our phylogenetic reconstruction (Fig. 6) based on the *COI* gene recovered *B. wadatsumi* sp. nov. as sister of *B. linseae*, the only congener with available molecular sequence, with moderate support (Bayesian posterior probability, BPP = 0.83). The two *Bathylepeta* species were recovered as sister to the genus *Iothia*, represented by three species. Although the support for the clade uniting *Bathylepeta* and *Iothia* was strong (BPP = 0.98), the genus *Iothia* was only weakly supported (BPP = 0.69). This clade formed a basal split with all other species at the base of Lepetidae, with the other clade including the genera *Lepeta*, *Limalepeta*, and *Sagamilepeta* being weakly supported (BPP = 0.60). *Lepeta* was found to be paraphyletic, with *Limalepeta lima* nested within it. However, the clade containing the three *Lepeta* species and *Limalepeta lima* was not well-supported (BPP < 0.60), and the internal relationships of this clade thus remain unresolved. The K2P genetic distance between *B. wadatsumi* sp. nov. and *B. linseae* was 9.4%, further supporting its status as a distinct species in the same genus.

Discussion

Systematics

Our molecular phylogeny (Fig. 6) supported the placement of *Bathylepeta wadatsumi* sp. nov. in the same genus as *B. linseae*, despite having overlapping basal plates. This confirms a wider range of variability in radula morphology in this genus than previously thought (Moskalev 1977; Schwabe 2006), leading to our emendation of the genus diagnosis to include slightly imbricating basal plates. Overall, the relationships among different lepetid genera in our tree were similar to those in a previous phylogenetic reconstruction combining *COI* and the nuclear histone-3 (*H3*) gene (Warén et al. 2011) – also recovering a basal split in the family between *Bathylepeta–Iothia* and the remaining genera included, as well as the paraphyly of *Lepeta*. Warén et al. (2011) treated *L. kuragiensis* as *Cryptobranchia kuragiensis*, but as the type species of *Cryptobranchia* is also *L. caeca* by monotypy (von Middendorff 1851), this name must be considered a junior synonym of *Lepeta*. Another solution, such as establishing a new genus to house *L. kuragiensis* and *L. concentrica*, is likely needed in the future to resolve the paraphyly of *Lepeta*.

Habitat of *Bathylepeta*

The discovery of *Bathylepeta wadatsumi* sp. nov. reveals the overlooked presence of a large-sized true limpet at abyssal depths in the northwestern Pacific. Our first *in situ* observation of the enigmatic lepetid genus *Bathylepeta* provides new insights into its habitat preferences, revealed as rocky substrates covered by thin sediment layers (Fig. 1B). This contrasts with previous assumptions that *Bathylepeta* lives on soft sediments, based on specimens of the other two species collected by epibenthic sledge (*B. laevis*) or Agassiz beam trawl (*B. linseae*) (Moskalev 1977; Schwabe 2006). *Bathylepeta laevis* was collected with foraminiferal silt (Moskalev 1977), while the habitat of *B. linseae* was assumed to be greyish-brown mud containing a small amount of diatoms and radiolarians – based on video images obtained by a towed camera and supplemented by sediments taken by multiple and box corers nearby (Schwabe 2006). However, towed gears cover a large surface area and cannot account for small-scale heterogeneity on the seafloor, such as small rock outcrops. The video cited for the habitat of *B. linseae* is from a separate deployment than the trawl that collected *B. linseae*, and towed gears are unlikely to land in the same track as deployments are impacted by currents. Given that true limpets are adapted to adhere to hard surfaces and cannot transverse muddy seafloor (Lindberg and Pearse 1990; Sigwart et al. 2019), it seems more likely that the earlier *Bathylepeta* specimens were dislodged from their natural rocky habitats during collection. A similar situation was recently pointed out for large monoplacophorans in the genus *Neopilina*, whose rocky habitat was revealed by submersible observations (Chen 2024; Sigwart et al. 2019).

Recent studies have emphasised that hard substrates are more prevalent in the abyssal plain than previously recognised, and they support distinct biological communities (Riehl et al. 2020). Small-scale heterogeneity in the abyssal seafloor can have great knock-on effects on the local biodiversity (Simon-Lledó et al. 2020). Traditional sampling methods such as dredges and beam trawls are often ineffective on rocky terrains (Lins and Brandt 2020; Sigwart et al. 2023), likely leading to an under-representation of *Bathylepeta* inhabiting these substrates which may be locally common. Our observation shows clear feeding trails and suggests *Bathylepeta* ingests sediments accumulated on their rocky substrate, which is in line with their muddy gut contents (Schwabe 2006). The body size of *Bathylepeta* is remarkable for the depth, and this genus could play an important role in utilising sedimentary carbon deposited on abyssal hard substrata.

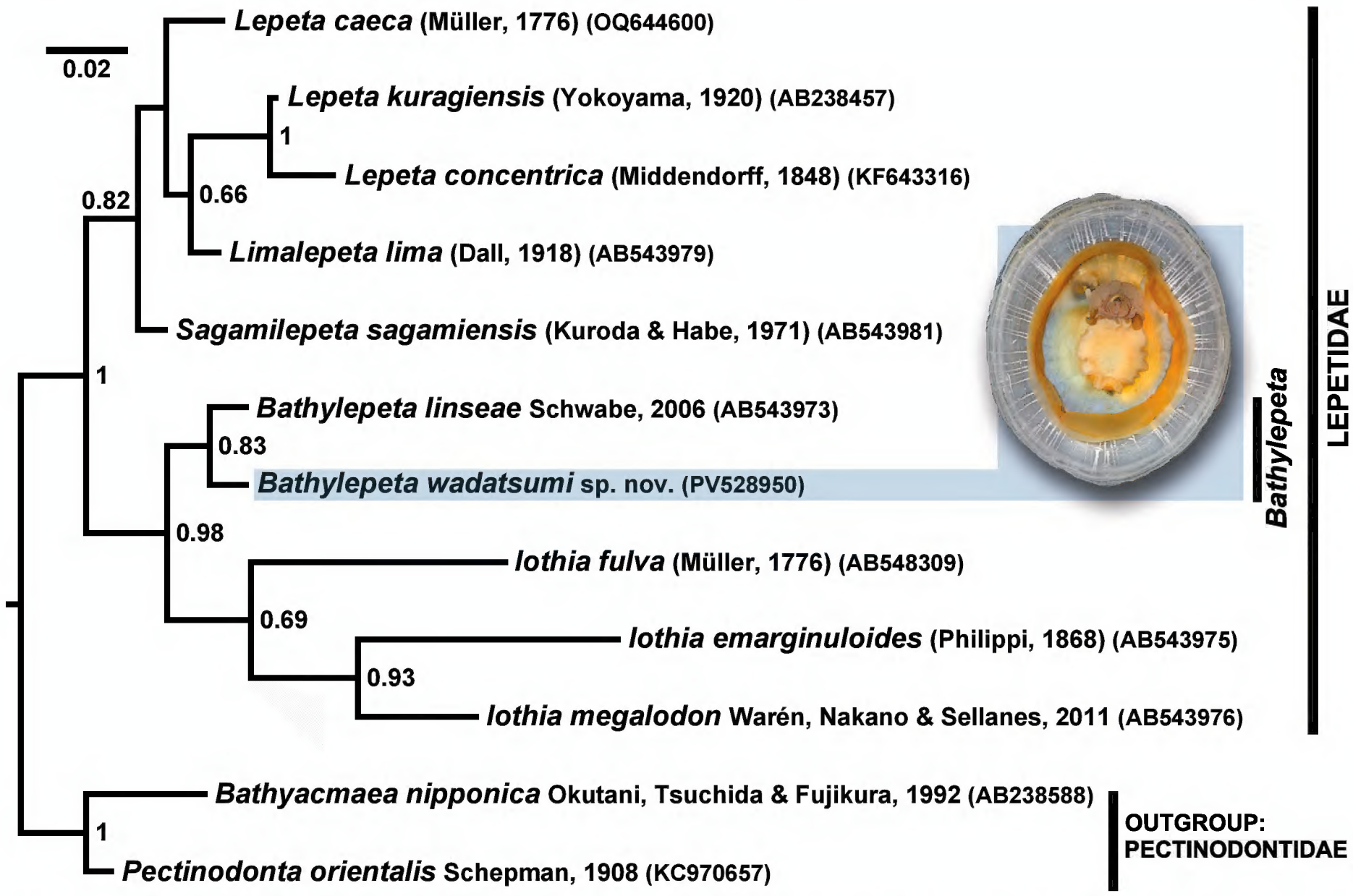

Figure 6. Molecular phylogeny of Lepetidae generated using Bayesian inference from 584 bp of the *COI* gene. Node values indicate Bayesian posterior probabilities (BPP); only those higher than 0.6 are shown.

Range of the genus

Our collection of a new *Bathylepeta* species off Japan significantly extends the known geographical range of the genus from Chile and the Weddell Sea in the southern hemisphere to the northwestern Pacific (Schwabe 2006). Furthermore, the sampling depth of 5922 m is deeper than that of *B. laevis* and marks the deepest bathymetric record so far for the entire Patellogastropoda (Moskalev 1977). This suggests a broad distribution for the genus, at least across the Pacific abyssal seafloor, with its presence in areas between Japan and Chile potentially obscured by the difficulty of sampling abyssal rocky substrates such as escarpments. The use of submersibles has been instrumental in accessing these habitats, allowing for direct observation and collection of organisms like *Bathylepeta* that were previously overlooked. Our finding underscores the need for more comprehensive explorations of rocky abyssal habitats using submersibles to reveal the true diversity and distribution of *Bathylepeta* and other animals relying on such habitats.

Author contributions

CC conceived and designed the study. CC carried out morphological investigations. MT undertook laboratory work for molecular sequencing. YI found and collected the specimen used in this study. CC analysed the molecular data. CC interpreted all data and drafted the original manuscript. All authors contributed to the final manuscript and gave final approval for its submission and publication in its current form.

Data availability

The DNA sequences newly generated in this work are available in NCBI GenBank under the accession number PV528950. The specimen studied has been deposited in the public collection of the National Museum of Nature and Science, Tsukuba (NSMT), Japan, under the catalogue number NSMT-Mo 79627.

Disclosure statement

No potential conflict of interest was reported by the authors.

Acknowledgements

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which reminds us that the greatest voyages are driven by freedom, camaraderie, and an insatiable thirst for discovery. Comments and edits from two anonymous reviewers improved an earlier version of this manuscript.

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